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STABILITY OF PERIODIC TRAVELLING WAVE SOLUTIONS OF A NERVE CONDUCTION EQUATION

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1. Introduction

In this paper we consider the nonlinear partial differential equation

$$\begin{aligned} u_t &= u_{xx} - f(u) - w, \\ w_t &= bu, \end{aligned} \quad b > 0, \quad -\infty < x < \infty. \quad (1)$$

This equation was introduced by FitzHugh [3] and Nagumo, Arimoto and Yoshizawa [5] as a simplified mathematical description of the excitation of nerve membrane and the propagation of nerve impulses on nerve axon. It is assumed that the nonlinear term $f(u)$ in Eq.(1) is a smooth function of u satisfying the following conditions:

$$\begin{aligned} f(0) &= 0, \quad f'(0) > 0, \\ f(u) &\begin{cases} > 0 & \text{for all } u \text{ in } (-\infty, 0) \cup (u_1, u_2), \\ \leq 0 & \text{elsewhere,} \end{cases} \end{aligned}$$

for certain $u_2 > u_1 > 0$, and

$$\int_0^{u_2} f(u) du < 0. \quad (2)$$

It is known that, if the value of $b > 0$ is sufficiently small, the partial differential equation (1) has two types of travelling wave solutions, i.e. pulse travelling wave solutions and periodic travelling wave solutions. The former solutions correspond to

solitary nerve impulses, and the latter solutions correspond to spatially periodic wave-trains of nerve impulses.

A travelling wave solution with a propagation speed $c \geq 0$ is a solution of Eq.(1) of the form

$$(u, w) = (\phi(z;c), \psi(z;c)), \quad z \equiv x + ct,$$

where ϕ and ψ are functions which may depend upon c . It follows that $(\phi(z;c), \psi(z;c))$ satisfies the ordinary differential equation

$$\begin{aligned} \phi_{zz} - c\phi_z - f(\phi) - \psi &= 0, \\ -c\psi_z + b\phi &= 0. \end{aligned} \quad (3)$$

A pulse travelling wave solution is a non-constant solution of (3) satisfying the condition

$$\lim_{|z| \rightarrow \infty} (\phi(z;c), \psi(z;c)) = (0, 0).$$

On the other hand, a periodic travelling wave solution is given as a periodic solution of (3).

It is proved by Evans [1] that Eq.(1) has two pulse travelling wave solutions with different propagation speeds c_1 and c_2 , $0 < c_1 < c_2$. They are called the slow pulse solution and the fast pulse solution respectively. The existence of the periodic travelling wave solutions is studied by Hastings [4]. He showed that Eq.(3) has a non-constant periodic solution if $b > 0$ is sufficiently small and the speed c is limited in a certain range.

Rinzel and Keller [6] studied numerically a case in which $f(u)$ is a piecewise-linear function of u given by

$$f(u) = \begin{cases} u & \text{for } u \leq a, \\ u - 1 & \text{for } u > a, \end{cases} \quad 0 < a < 0.5. \quad (4)$$

They showed that, in this case, Eq.(3) has a non-constant periodic solution $(\phi(z;c), \psi(z;c))$ if c is limited in the range $c_1 < c < c_2$. This periodic solution depends smoothly on c and its minimum period $L(c)$ is a smooth function of c . The form of $L(c)$, in the case the parameter a in (4) is not so small, is shown in Fig.1. (See Fig.8 in Rinzel and Keller [6].) In this case, $L(c)$ is defined on the interval (c_1, c_2) and it satisfies

$$L'(c) \begin{cases} < 0 & \text{for } c_1 < c < c_0, \\ = 0 & \text{for } c = c_0, \\ > 0 & \text{for } c_0 < c < c_2, \end{cases}$$

where c_0 is a certain point in (c_1, c_2) . Moreover it satisfies

$$\lim_{c \rightarrow c_1+0} L(c) = \lim_{c \rightarrow c_2-0} L(c) = +\infty.$$

Namely the periodic solution $(\phi(z;c), \psi(z;c))$ tends to the fast pulse solution as $c \rightarrow c_2-0$ and to the slow pulse solution as $c \rightarrow c_1+0$.

On the other hand, if the parameter a in (4) is very small, the function $L(c)$ is of the form shown in Fig.2. Namely, $L(c)$ is defined on the interval (c_{\min}, c_2) , where c_{\min} is a certain

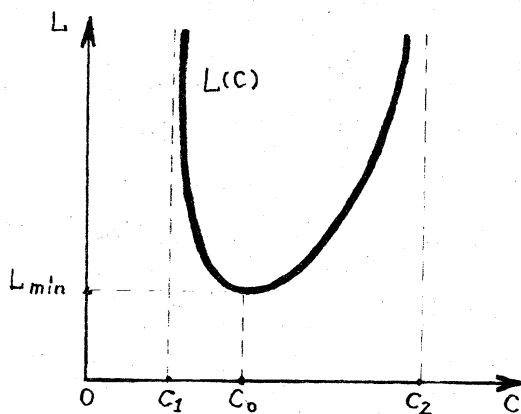


Fig. 1.

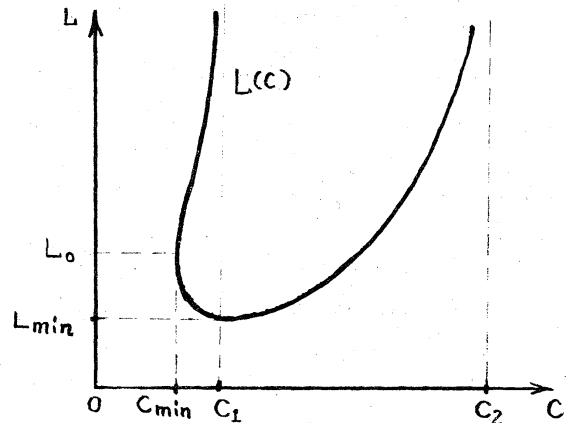


Fig. 2.

positive number smaller than c_1 . It is a double-valued function of c on the range (c_{\min}, c_1) , i.e. there exist two periodic travelling wave solutions with the same propagation speed c , $c_{\min} < c < c_1$, and with different spatial periods. These are called the long periodic solution and the short periodic solution respectively. The long periodic solution tends to the slow pulse solution as $c \rightarrow c_1 - 0$.

Let L_{\min} denote the minimum of the function $L(c)$. For any positive number ℓ such that $\ell > L_{\min}$, there exist two values of c , say \bar{c}_1 and \bar{c}_2 , satisfying

$$L(\bar{c}_1) = L(\bar{c}_2) = \ell, \quad 0 < \bar{c}_1 < \bar{c}_2 < c_2.$$

This implies that Eq.(1) has two periodic travelling wave solutions with the same spatial period ℓ and with different propagation speeds \bar{c}_1 and \bar{c}_2 . They are called the slow ℓ -periodic solution and the fast ℓ -periodic solution respectively.

Let us consider the case where $f(u)$ is a smooth function satisfying the condition (2). If $f(u)$ is not deviated largely from the peicewise-linear function given by (4), the speed vs period characteristic $L(c)$ of the periodic travelling wave solution $(\phi(z;c), \psi(z;c))$ may be similar to the ones shown in Fig.1 and in Fig.2, and hence Eq.(1) may have a slow ℓ -periodic solution and a fast ℓ -periodic solution if $\ell > L_{\min}$.

Rinzel and Keller [6] showed by numerical analysis that, in the case $f(u)$ is the piecewise-linear function, the slow ℓ -periodic solution is always unstable. It is conjectured that this statement holds even if $f(u)$ is not restricted to the piecewise-linear function.

In this paper, we prove a theorem which ascertains that a periodic travelling wave solution $(\phi(z;c), \psi(z;c))$ is unstable

if its spatial period $L(c)$ satisfies $L'(c) < 0$. This theorem justifies a part of the above conjecture, i.e. we can conclude by the use of this theorem that the slow ℓ -periodic solution is unstable if the function $L(c)$ is of the form shown in Fig.1, and that, in the case $L(c)$ is as shown in Fig.2, the slow ℓ -periodic solution is unstable if ℓ is limited in the range $L_1 > \ell > L_{\min}$, where L_1 is as shown in Fig.2.

2. Preliminaries for Stability Analysis

We introduce the travelling coordinate system

$$z = x + ct, \quad t = t,$$

in which Eq.(1) takes the form

$$u_t = u_{zz} - cu_z - f(u) - w,$$

$$w_t = -cw_z + bu.$$

The periodic travelling wave solution $(u, w) = (\phi(z;c), \psi(z;c))$ is a stationary solution of this equation.

Since (3) is an autonomous system, we can replace the solution $(\phi(z;c), \psi(z;c))$ by its translate $(\phi(z+h;c), \psi(z+h;c))$, where h is an arbitrary real constant. Hence, in order to fix the solution $(\phi(z;c), \psi(z;c))$, we need to "normalize the phase" by an appropriate condition. We fix the phase by demanding that

$$\phi(0;c) = 0, \quad \phi_z(0;c) > 0.$$

Let us consider the linealized perturbation equation of the above system with respect to this stationary solution, i.e.

$$\begin{aligned} \hat{U}_t &= \hat{U}_{zz} - c\hat{U}_z - f'(\phi(z;c))\hat{U} - \hat{W}, \\ \hat{W}_t &= -c\hat{W}_z + b\hat{U}. \end{aligned}$$

This equation has a solution of the form

$$(\hat{U}(z,t), \hat{W}(z,t)) = e^{\lambda t} (U(z;\lambda), W(z;\lambda)),$$

where $(U(z;\lambda), W(z;\lambda))$ is a solution of the linear ordinary differential equation

$$\begin{aligned} \lambda U &= Y_{zz} - cU_z - f'(\phi(z;c))U - W, \\ \lambda W &= -cW_z + bU, \end{aligned} \quad (5)$$

where λ is a complex number. Assume that there exists a complex number λ with $\text{Re}\{\lambda\} > 0$ such that Eq.(5) has a non-trivial solution $(U(z;\lambda), W(z;\lambda))$ which is bounded for all z in $(-\infty, \infty)$. In this case, the perturbation equation has a solution which grows exponentially in the course of time even if the initial disturbance is sufficiently small. Hence the travelling wave solution $(\phi(z;c), \psi(z;c))$ is unstable in this case.

Equation (5) can be rewritten as

$$\frac{d}{dz} \mathbf{v} = A(z;\lambda,c) \mathbf{v}, \quad (6)$$

where

$$\mathbf{v} \equiv \begin{pmatrix} U \\ U_z \\ W \end{pmatrix}, \quad A(z;\lambda,c) \equiv \begin{pmatrix} 0 & 1 & 0 \\ \lambda + f'(\phi(z;c)) & c & 1 \\ b/c & 0 & -\lambda/c \end{pmatrix}.$$

Let $X(z;\lambda,c)$ be a matrix defined by the matrix differential equation $\frac{d}{dz} X = AX$ with the initial condition $X(0;\lambda,c) = E$. Since the coefficient matrix $A(z;\lambda,c)$ is an $L(c)$ -periodic function of z , it follows from Floquet's theory that Eq.(5) has a bounded non-trivial solution if and only if one of the eigenvalues of $X(L(c);\lambda,c)$ is of modulus 1. Hence the next lemma holds.

Lemma 1. A periodic travelling wave solution $(\phi(z;c), \psi(z;c))$ is

unstable if, for some complex number λ satisfying $\operatorname{Re}\{\lambda\} > 0$, the matrix $X(L(c); \lambda, c)$ has an eigenvalue whose modulus is 1.

Let $\phi(z; c)$ be an $L(c)$ -periodic vector function of z defined by

$$\phi(z; c) \equiv (\phi(z; c), \phi_z(z; c), \psi(z; c))',$$

where the ' denotes a transposition of a vector. The following equality is obtained by differentiating (3) with respect to z .

$$\begin{aligned} (\phi_z)_{zz} - c(\phi_z)_z - f'(\phi)\phi_z - \psi_z &= 0, \\ -c(\psi_z)_z + b\phi_z &= 0. \end{aligned} \quad (7)$$

This implies that the vector function $\phi_z(z; c)$, which is an $L(c)$ -periodic function of z , satisfies the equation

$$\frac{d}{dz} \phi_z(z; c) = A(z; 0, c) \phi_z(z; c).$$

Hence the following equalities hold in the case of $\lambda = 0$.

$$\phi_z(0; c) = \phi_z(L(c); c) = X(L(c); 0, c) \phi_z(0; c). \quad (8)$$

Let $\mu_i(\lambda, c)$ and $p_i(\lambda, c)$, $i = 1, 2, 3$, denote the eigenvalues and the corresponding eigenvectors of the matrix $X(L(c); \lambda, c)$, respectively. By virtue of (8), we may assume without losing generality that

$$\mu_1(0, c) = 1, \quad p_1(0, c) = \phi_z(0; c). \quad (9)$$

The following equality is obtained by the use of Jacobi's formula.

$$\begin{aligned} \det\{X(z; \lambda, c)\} &= \det\{X(0; \lambda, c)\} \exp\left[\int_0^z \operatorname{tr} A(z; \lambda, c) dz\right] \\ &= \exp\{(c - \lambda/c)z\}. \end{aligned}$$

Hence, in the case of $\lambda = 0$, we obtain

$$\mu_1(0, c) \mu_2(0, c) \mu_3(0, c) = \exp\{cL(c)\}.$$

since $c > 0$, $L(c) > 0$ and $\mu_1(0, c) = 1$, it follows that

$$\mu_2(0, c)\mu_3(0, c) > 1.$$

3. Stability of Periodic Travelling Wave Solutions

The following theorem is a main result of this paper.

Theorem. A periodic travelling wave solution $(\phi(z; c), \psi(z; c))$ is unstable if its spatial period $L(c)$ satisfies $L'(c) < 0$.

This theorem is obtained as a result of two lemmas which are formulated below. The first lemma is as follows.

Lemma 2.

$$\left. \frac{\partial}{\partial \lambda} \mu_1(\lambda, c) \right|_{\lambda=0} = -L'(c). \quad (11)$$

Proof. Since $\phi(z; c)$ is an $L(c)$ -periodic function of z , it satisfies the equality

$$\phi(L(c); c) = \phi(0; c).$$

By differentiating this equality with respect to c , we obtain

$$\phi_z(L(c); c)L'(c) + \phi_c(L(c); c) = \phi_c(0; c). \quad (12)$$

Let $(U, W) = (\bar{U}(z; \lambda, c), \bar{W}(z; \lambda, c))$ be a solution of Eq.(5) subject to the initial condition

$$\bar{V}(0; \lambda, c) = \phi_z(0; c) + \lambda \phi_c(0; c), \quad (13)$$

where

$$\bar{V}(z; \lambda, c) \equiv (\bar{U}(z; \lambda, c), \bar{U}_z(z; \lambda, c), \bar{W}(z; \lambda, c))'.$$

Since $(U, W) = (\phi_z(z; c), \psi_z(z; c))$ is a non-trivial solution of Eq.(5) in the case of $\lambda = 0$, it follows from (13) that

$$\bar{V}(z; 0, c) = \phi_z(z; c). \quad (14)$$

Let us limit the range of the variable z in the finite interval $[0, L(c)]$. We can define the partial derivatives $(\bar{U}_\lambda(z; \lambda, c), \bar{W}_\lambda(z; \lambda, c))$ and $(\phi_c(z; c), \psi_c(z; c))$ for all z in $[0, L(c)]$. The following equalities are obtained by substituting $(U, W) = (\bar{U}(z; \lambda, c), \bar{W}(z; \lambda, c))$ in (5), then differentiating (5) with respect to λ , setting $\lambda = 0$ and using (14).

$$\begin{aligned}
 & \phi_z(z; c) \\
 &= \{\bar{U}_\lambda(z; 0, c)\}_{zz} - c\{\bar{U}_\lambda(z; 0, c)\}_z - f'(\phi(z; c))\bar{U}_\lambda(z; 0, c) \\
 & \quad - \bar{W}_\lambda(z; 0, c), \\
 & \psi_z(z; c) \\
 &= -c\{\bar{W}_\lambda(z; 0, c)\}_z + b\bar{U}_\lambda(z; 0, c).
 \end{aligned} \tag{15}$$

On the other hand, the following equalities are obtained by differentiating (3) with respect to c .

$$\begin{aligned}
 & \phi_z(z; c) \\
 &= \{\phi_c(z; c)\}_{zz} - c\{\phi_c(z; c)\}_z - f'(\phi(z; c))\phi_c(z; c) - \psi_c(z; c), \\
 & \psi_z(z; c) \\
 &= -c\{\psi_c(z; c)\}_z + b\phi_c(z; c).
 \end{aligned}$$

The initial condition (12) yields that

$$\bar{v}_\lambda(0; 0, c) = \phi_c(0; c).$$

Hence it follows from (15) and (16) that

$$\bar{v}_\lambda(z; 0, c) = \phi_c(z; c), \quad 0 \leq z \leq L(c).$$

Thus the following equality holds as $\lambda \rightarrow 0$.

$$\bar{v}(z; \lambda, c) = \phi_z(z; c) + \lambda\phi_c(z; c) + O(\lambda^2), \tag{17}$$

$$0 \leq z \leq L(c).$$

Taking into account of (17) and the equality

$X(z; \lambda, c) \bar{V}(0; \lambda, c) = \bar{V}(z; \lambda, c)$, we obtain

$$\begin{aligned} & X(L(c); \lambda, c) \{ \phi_z(0; c) + \lambda \phi_c(0; c) \} \\ &= \phi_z(L(c); c) + \lambda \phi_c(L(c); c) + O(\lambda^2). \end{aligned}$$

Hence, by virtue of (8) and (12), the following equality holds as $\lambda \rightarrow 0$.

$$\begin{aligned} & X(L(c); \lambda, c) \{ \phi_z(0; c) + \lambda \phi_c(0; c) \} \\ &= \{1 - \lambda L'(c)\} \{ \phi_z(0; c) + \lambda \phi_c(0; c) \} + O(\lambda^2). \end{aligned}$$

This equality, together with (8), implies that

$$\left. \frac{\partial}{\partial \lambda} p_1(\lambda, c) \right|_{\lambda=0} = \phi_c(0; c)$$

and

$$\left. \frac{\partial}{\partial \lambda} \mu_1(\lambda, c) \right|_{\lambda=0} = -L'(c).$$

Q.E.D.

Next let us consider the eigenvalue $\mu_i(\lambda, c)$, $i = 1, 2, 3$, of the matrix $X(L(c); \lambda, c)$ in the case where λ is a sufficiently large positive number.

Lemma 3. If λ is a sufficiently large positive number, two eigenvalues of $X(L(c); \lambda, c)$ have module < 1 and one has modulus > 1 .

Proof. The coefficient matrix $A(z; \lambda, c)$ of Eq. (6) can be written as

$$A(z; \lambda, c) = C(\lambda, c) + D(z; c),$$

where

$$C(\lambda, c) \equiv \begin{pmatrix} 0 & 1 & 0 \\ \lambda & c & 1 \\ b/c & 0 & -\lambda/c \end{pmatrix}, \quad D(z; c) \equiv \begin{pmatrix} 0 & 0 & 0 \\ f'(\phi(z; c)) & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

Let $v_i(\lambda, c)$ and $r_i(\lambda, c)$, $i = 1, 2, 3$, denote the eigenvalues and

the corresponding eigenvectors of the matrix $C(\lambda, c)$, respectively.

It is easily shown that $v_i(\lambda, c)$ satisfy

$$\begin{aligned} v_1(\lambda, c) &= -\lambda/c + O(1), \\ v_2(\lambda, c) &= -\sqrt{\lambda} + O(1), \quad v_3(\lambda, c) = \sqrt{\lambda} + O(1) \end{aligned} \quad (18a)$$

as $\lambda \rightarrow +\infty$, and that $r_i(\lambda, c)$ are given by

$$r_i(\lambda, c) = (1, v_i, v_i^2 - cv_i - \lambda)'. \quad (18b)$$

Let $R(\lambda, c)$ be a non-singular matrix defined by

$$R(\lambda, c) \equiv [r_1(\lambda, c), r_2(\lambda, c), r_3(\lambda, c)],$$

and $Y(z; \lambda, c)$ be a matrix defined by

$$Y(z; \lambda, c) \equiv \{R(\lambda, c)\}^{-1} X(z; \lambda, c) R(\lambda, c).$$

Clearly the eigenvalues of $Y(L(c); \lambda, c)$ are given by $\mu_i(\lambda, c)$. It follows that $Y(z; \lambda, c)$ satisfies the differential equation

$$\begin{aligned} \frac{d}{dz} Y(z; \lambda, c) &= \{R(\lambda, c)\}^{-1} A(z; \lambda, c) R(\lambda, c) Y(z; \lambda, c) \\ &= \{\Lambda(\lambda, c) + \bar{D}(z; \lambda, c)\} Y(z; \lambda, c), \end{aligned}$$

where $\Lambda(\lambda, c)$ and $\bar{D}(z; \lambda, c)$ are matrices given by

$$\Lambda(\lambda, c) \equiv \begin{pmatrix} v_1(\lambda, c) & 0 & 0 \\ 0 & v_2(\lambda, c) & 0 \\ 0 & 0 & v_3(\lambda, c) \end{pmatrix},$$

$$\bar{D}(z; \lambda, c) \equiv \{R(\lambda, c)\}^{-1} D(z; c) R(\lambda, c).$$

It is easily verified by the use of (18a,b) that all the elements of $\bar{D}(z; \lambda, c)$ vanish as $\lambda \rightarrow +\infty$. Hence the eigenvalues of $Y(L(c); \lambda, c)$ do not deviate largely from

$$\exp\{v_i(\lambda, c)L(c)\}, \quad i = 1, 2, 3,$$

as $\lambda \rightarrow +\infty$. Thus it follows from (18a) that two eigenvalues of $X(L(c); \lambda, c)$ have module < 1 and one has modulus > 1 .

Q.E.D.

Let us complete the proof of Theorem.

Proof of Theorem. Assume that $L'(c) < 0$. In this case, it follows from (9) and (11) that the eigenvalue $\mu_1(\lambda, c)$ of $X(L(c); \lambda, c)$ satisfies

$$\mu_1(\lambda, c) > 1$$

if λ is a sufficiently small positive number. Moreover it follows from (10) that

$$|\mu_2(\lambda, c)| > 1 \quad \text{or} \quad |\mu_3(\lambda, c)| > 1$$

when $|\lambda|$ is sufficiently small. Hence, at least two eigenvalues of $X(L(c); \lambda, c)$ have module > 1 when λ is a sufficiently small positive number. On the other hand, Lemma 3 claims that two eigenvalues of $X(L(c); \lambda, c)$ have module < 1 as $\lambda \rightarrow +\infty$. Hence it follows that one of the eigenvalues must have modulus $= 1$ for some $\lambda > 0$. Therefore, according to Lemma 1, the travelling wave solution $(\phi(z; c), \psi(z; c))$ is unstable in this case.

Q.E.D.

[1] Evans, J. W.: Nerve axon equations: IV. The stable and the unstable impulses. Indiana Univ. Math. J. 22, 1169-1190(1975) [2] Evans, J. W.: Nerve axon equations: III. Stability of the nerve impulse. Indiana Univ. Math. J. 22, 577-593 (1972) [3] FitzHugh, R.: Mathematical models of excitation and propagation in nerve, in Biological Engineering (Schwan, H. P., ed), 1-85. New York; McGraw-Hill 1969. [4] Hastings, S.: The existence of periodic solutions to Nagumo's equation. Quart. J. Math. Oxford(3), 25, 369-378(1974) [5] Nagumo, J., Arimoto, S., Yoshizawa, S.: An active pulse transmission line simulating nerve axon, Proc. IRE. 50, 2061-2070(1962) [6] Rinzel, J., Keller, J. B.: Travelling wave solutions of a nerve conduction equation. Biophys. J. 13, 1313-1337(1973)